# *Dermatophagoides farinae*: The Digestive System[1]

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**Abstract:** The digestive system of the house-dust mite was studied by means of light microscopy, and transmission and scanning electron microscopy. The system consists of: 1) a prebuccal cavity which is surrounded by mouthparts comprising a gnathosoma, 2) a cuticle-lined foregut which consists of a muscular pharynx and a thin-walled esophagus, 3) a microvillous midgut which is divided into a large anterior portion with two caeca and a bulbous posterior section, and 4) a cuticle-lined hindgut consisting of a broad anterior portion and a narrow posterior section. The relationships of the mouthparts, the morphology of the systematic components, and the varying cell types are demonstrated. Discussed are possible digestive processes including formation of a peritrophic membrane and the production of salivary secretions which originate in the idiosoma and are channeled anteriorly to be utilized in the prebuccal cavity. An attempt is made to homologize the diverse nomenclature previously used for naming the gut regions of the Acari.

## INTRODUCTION

The arthropod digestive system is remarkably constant in terrestrial forms (Barrington, 1967). It consists of a foregut, midgut, and hindgut, and each section may be further subdivided. The foregut is cuticle-lined while the midgut lacks a cuticular lining. The hindgut is usually lined with a cuticle along its entire length and always terminates with a cuticular lined section. Malpighian tubules, if present, enter the gut at the junction of the mid- and hindguts.

Insects have been extensively studied, and portions of the gut of several insects have been observed with the electron microscope. Among these studies are a book by Smith (1968) and articles by Peters (1969) and Richards and Richards (1971).

Typical arachnid digestion has been described (Mitchell, 1970), and digestion in a phalangid has been studied (Phillipson, 1961).

The anatomy of the digestive system, in whole or in part, of different groups of mites has been studied at the level of resolution of the light microscope

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(Michael, 1901; Reuter, 1909; Bader, 1938; Vitzthum, 1940; Blauvelt, 1945; Hughes, 1954; Perron, 1954; Johnston, 1965; Prasse, 1967; Rohde and Oemick, 1967; Kuo and Nesbitt, 1970). Fine structure studies on the digestive tracts of mites have been reported (Wright and Newell, 1964; and Whitmoyer *et al.*, 1972).

It is the purpose of this study to describe the digestive system of *Dermatophagoides farinae* Hughes, a mite which has been associated with the allergen in house dust (Mitchell *et al.*, 1969). The formation of food balls and the fine structure of the peritrophic membrane of *D. farinae* have been reported by Wharton and Brody (in press).

## MATERIALS AND METHODS

Mites cultured by the Acarology Laboratory were used. *D. farinae* was kept in small jars at constant 75% relative humidity at room temperature by means of desiccators containing a saturated solution of sodium chloride (Larson *et al.*, 1969). Most of the mites studied here were cannibalistic (Portions of the cuticle of ingested mites were almost invariably seen in the mid- and hindgut). The mites were removed from the tops of cultures where other mites were the only source of food.

Mites were removed from the culture jars and studied in several ways. 1) Living mites were studied under the dissecting microscope to observe gross movements of feeding behavior and by scanning electron microscopy (SEM) to study surface details. Living mites were placed on glass slides in two drops of Crown® immersion oil, covered with a cover slip, and observed by phase contrast and bright-field microscopy. 2) Whole mounts were cleared in Nesbitt's solution, mounted on glass slides in Hoyer's mounting medium, and observed by phase contrast microscopy. All the mouth parts and sclerotized portions of the digestive tract can be observed in whole mounts. 3) Thick sections (1 to 3 microns) of plastic embedded mites were studied by phase contrast and bright field microscopy. Sagittal and cross sections were cut through whole mites (which had been prepared for sectioning according to procedures described below) and stained for 30 sec with Azure B solution. 4) Thin sections (350 to 900 Å) were studied by means of transmission electron microscopy (TEM). In preparing specimens for TEM, living mites were fixed in 12.5% glutaraldehyde at room temperature and then postfixed in 1% osmium tetroxide at pH 7.4. Primary aldehyde fixation was from 5 hr to overnight, followed by postfixation in 0.1M cacodylate buffered osmium for 5 to 8 hr; these extended fixation periods gave better results. After fixation and before embedding, the mites were dehydrated in a graded series of ethyl alcohols (50, 70, 95, 100%). The mites were left for at least 10 min in the 50% to 95% range, and 20 to 30 min in the absolute alcohol. Propylene oxide was the most satisfactory transitional solvent. A mixed resin (catalyzed with DMP-30) of

Epon 812 and Araldite 502 was used in the following proportions (propylene oxide to resin): 3:1 for 1 hr, 2:2 for 1 hr, 1:3 overnight, and then 24 hr in 100% fresh resin before final embedment in fresh plastic in an oven at 60°C for 2 to 3 days. Glass knives were used to cut cross sections on a Porter-Blum MT-2 ultramicrotome. Sections were picked up on 100- or 200-mesh, parlodion-coated copper grids and stained with uranyl acetate and lead citrate. Thin sections were examined on an RCA transmission electron microscope model EMU-3G.

Whole mites were examined on a Cambridge scanning electron microscope, model Mark 2a. Live, uncoated mites, or mites treated with Gylcerol-KCL (Brody and Wharton, 1971) were stuck to specimen stages with carbon paint. Live specimens were mounted one day previous to observation to assure proper orientation and were kept alive by covering the specimen stage with a vial containing a small piece of moist cotton.

## RESULTS

The digestive system of the house-dust mite (Fig. 1) begins anteriorly with a prebuccal cavity which is surrounded by mouthparts comprising a gnathosoma (Fig. 2). The cuticle-lined foregut follows the prebuccal space and consists of a muscular pharynx and thin walled esophagus (Fig. 1). The next section of the system is the midgut which is lined with microvillous epithelium and is divided into two sections, a large anterior portion with two caeca and a bulbous posterior section (Fig. 1). The hindgut is lined with cuticle and has a broad anterior portion and a narrow posterior section portion which leads to the anal

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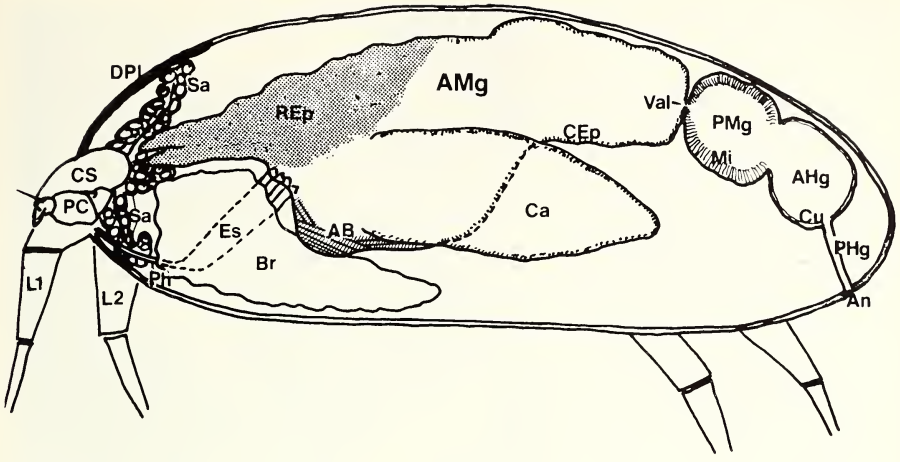
### FIGURE KEY

A = apophysis; AB = active bands; AC = attached cell; AHg = anterior hindgut; AMg = anterior midgut; An = anus; AP = anal plate; B = buccal space; BM = basement membrane; BP = basal podomere; Br = brain; C = channel; Ca = caecum; CAB = cell of active bands; CEp = cuboidal epithelium; CF = cuticular fold; CM = cell membrane; CMu = circular muscles; CnMu = constrictor muscle; CS = cheliceral shaft; Cu = cuticle; DM = dilator muscle; DP = distal podomere; DPl = dorsal plate; E = epistome; Egg = egg; ECu = esophageal cuticle; Ep = epithelium; Epc = epicuticle; ER = endoplasmic reticulum; Es = esophagus; F = longitudinal fold; FB = food ball; FeB = fecal ball; FC = free cell; FD = fixed digit; H = hypostome; Ha = haemocoel; HP = hypostomal process; IC = ingested cuticle; L = labrum; $L_1$,$L_2$ = leg one, leg two; LR = lateral reflection; Ly = lysosome; M = microorganisms; MD = movable digit; Mi = microvilli; Mit = mitochondria; MR = median ridge; Mu = muscle; Muc = mucous-like lining; N = nucleus; PC = palp coxa; PCa = pore canal; Ph = pharynx; PHg = posterior hindgut; PM = peritrophic membrane; PMg = posterior midgut; R = cuticular ridge; Re = reproductive system; REp = reduced epithelium; S = solenidion; Sa = salivary gland; SCu = sloughed cuticle; Se = seta; SG = supracoxal gland; Sh = sheath; SL = separating layer; T = trough; Te = tendon; V = venter; Va = vacuole; Val = valve.



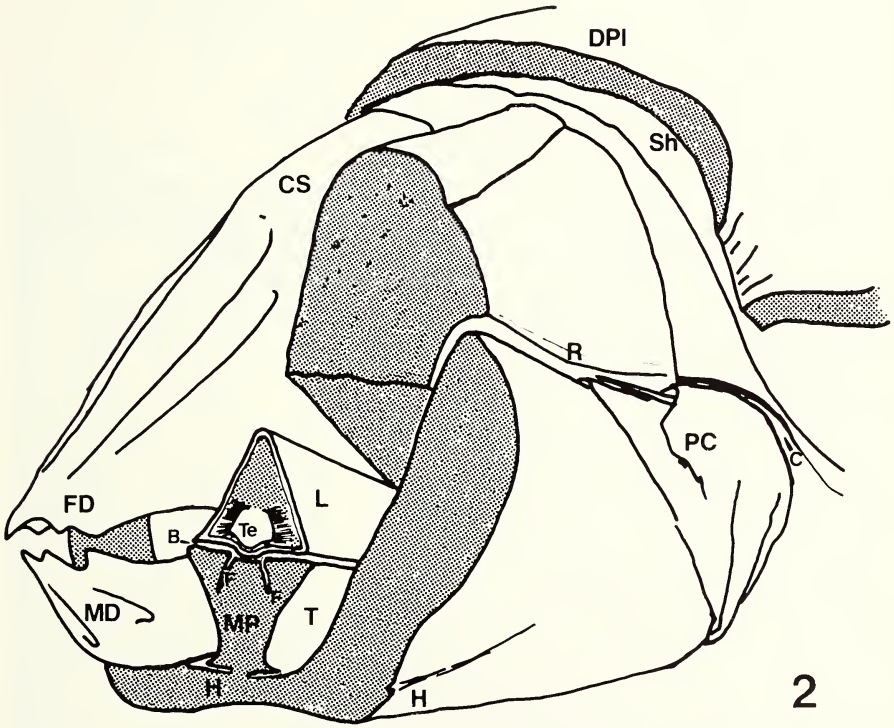
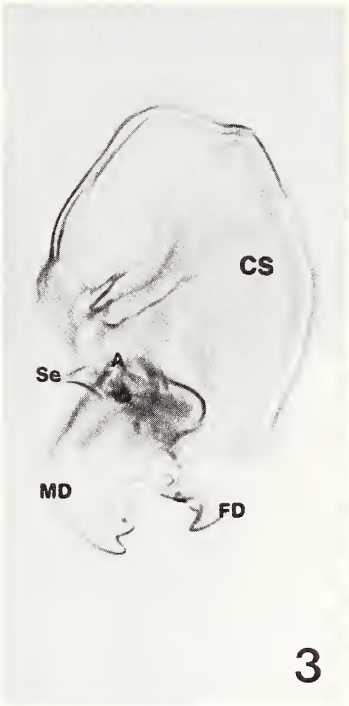




Fig. 1. Diagram representing a sagittal section through an adult female house-dust mite demonstrating the gross components of the digestive system. × 220.

Fig. 2. Diagram of a cross section of the gnathosoma revealing the prebuccal cavity and surrounding mouthparts. An intact chelicera remains in its relative position. × 2,000.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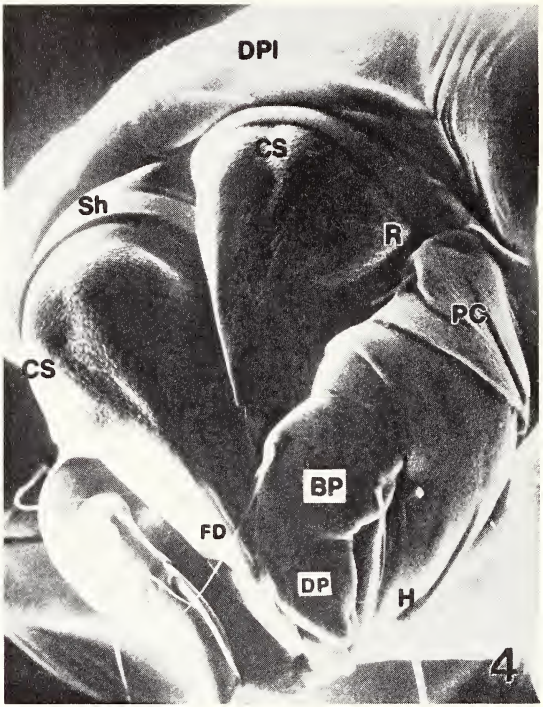
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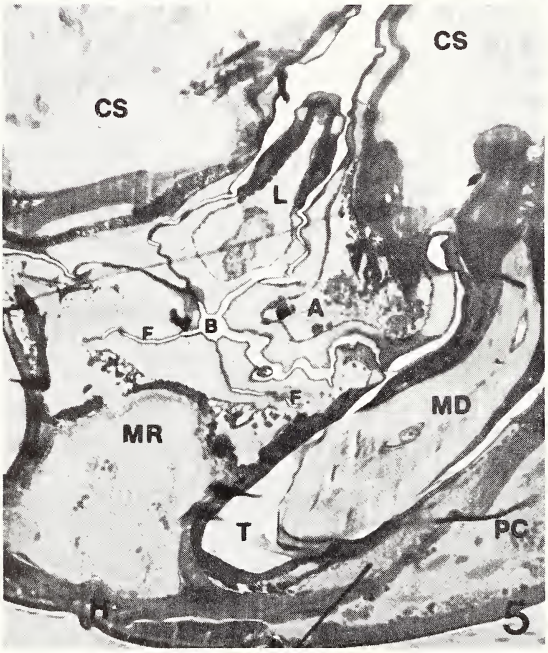
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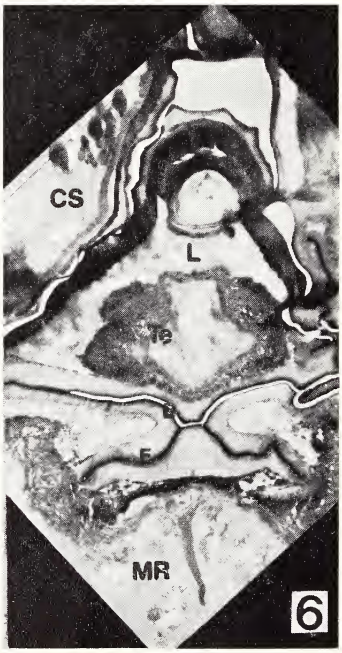
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opening (Fig. 1). Salivary glands are found associated with the digestive system (Fig. 1).

The gnathosoma is the anterior functional unit of the digestive system. It is articulated at the perignathosomal[4] furrow with the rest of the body known as the idiosoma (Fig. 1). The gnathosoma of *D. farinae* is approximately one-fifth the length of the idiosoma and is composed of two dorsal chelicerae, an epistome that supports the medial-anteriorly projected labrum, a ventral hypostome, and two lateral pedipalps (Fig. 2). Anteriorly these gnathosomal components surround the prebuccal space and posteriorly they surround the anterior one-fourth of the pharynx.

Each heavily sclerotized chelicera is oval in cross section and tapers anteriorly in width (from 35 microns posteriorly to 10 microns anteriorly) and height (from 40 microns posteriorly to 30 microns anteriorly). It consists of two segments (Fig. 3). The basal segment has a proximal shaft that is a hollow, oblate, truncated cone to which is attached a distal fixed digit. The movable digit is the second segment and it articulates with the cheliceral shaft proximal to the fixed digit so that the digits are in opposition. The natural position of the chelicerae is such that the dorsal aspects of the shafts are actually the anterior face of the gnathosoma, and the movable digit is posterior to the fixed digit (Fig. 4). On the shaft are two medial apophyses; one is rather small, blunt and centrally located on the shaft, while the other is just posterior to the point of articulation of the movable digit and has a heavy base which tapers to a narrow tip directed anteromedially. The single spike-like seta on the chelicera is slightly posterior and ventral to the larger apophysis and is also directed anteromedially (Fig. 3). A heavy dorsolateral cuticular ridge runs along one-third of the length of the cheliceral shaft (Figs. 2 and 4). The chelicerae are provided with intrinsic and extrinsic musculature as described for *Caloglyphus berlesei* by Johnston (1965). The extrinsic musculature includes powerful

[4] This furrow is most frequently designated circumcapitular. It is recommended that "circumcapitular" be replaced for the same reason that "capitulum" has been retired.

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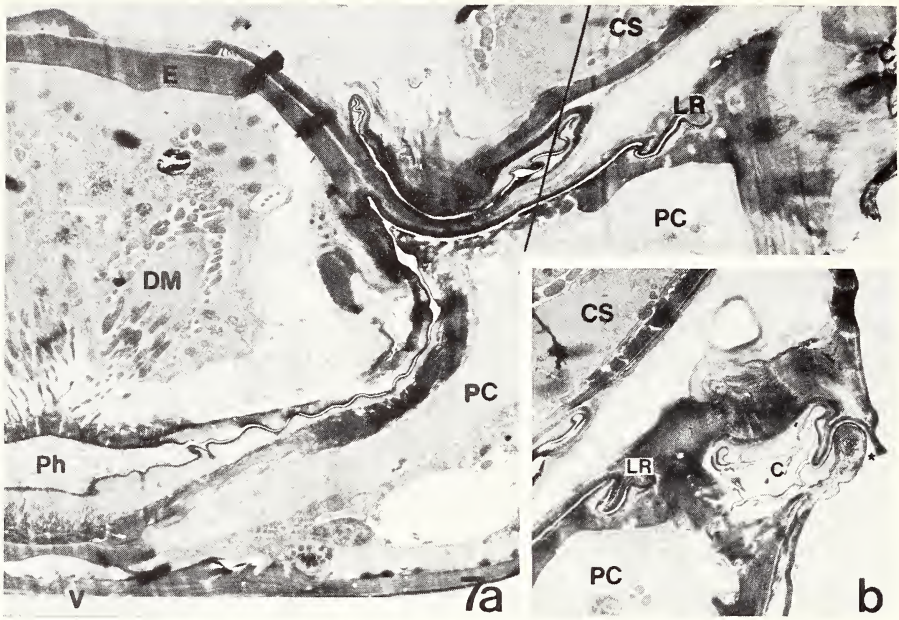
Fig. 3. Photomicrographs showing a medial view of an excised chelicera. × 1,000.

Fig. 4. Scanning electron micrograph (SEM) of an anterior view of the gnathosoma. Note that the right chelicera is extended while the left one is retracted. × 1,000.

Fig. 5. Transmission electron micrograph (TEM) of a cross section through the gnathosoma. The movable digit (MD) of the retracted chelicera is accommodated by a trough (T) formed from the median ridge (MR) of the hypostome (H) and the palpal coxa (PC). × 2,000.

Fig. 6 TEM of cross section through labrum (L) as it covers the prebuccal space (B). The presence of longitudinal folds (F) is a constant on the dorsal surface of the hypostomal median ridge (MR). × 2,000.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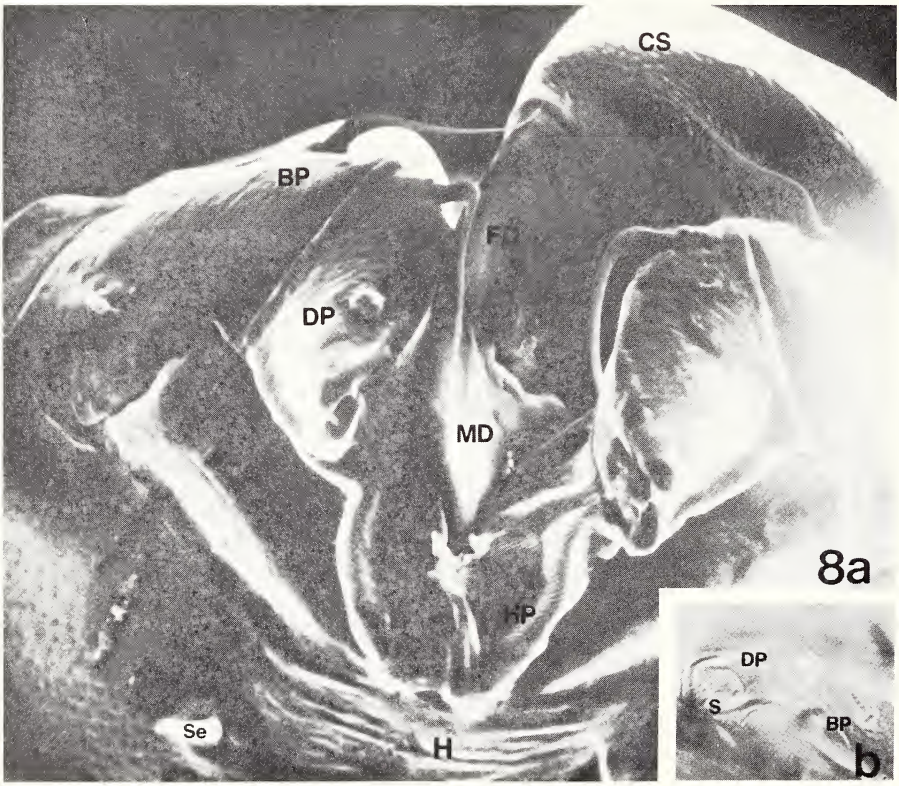
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retractor muscles which insert on the ventral surface of the shaft and originate on the ventral surface of the idiosomal dorsal plate. The levator and depressor muscles provide intrinsic opening and closing action to the movable digit. The chelicerae articulate with the idiosoma by a complex synarthrodial membrane known as the cheliceral sheath. The sheath is attached to the cheliceral shaft (which is about 70 microns long) about 33 microns from its posterior margin (Figs. 2 and 4). The sheath extends forward for a short distance and then doubles back on itself. Dorsally and laterally the sheaths are continuous with the synarthrodial cuticle of the perignathosomal suture. The sheaths accommodate increased mobility of the chelicerae and permit independent movement of each chelicera by virtue of the fact that the sheaths are independent of each other. At the ventral surfaces of the cheliceral shafts, the sheaths are reduced to a simple synarthrodial membrane. The ventral articulation of each chelicera appears to be hinge-like so that a sheath is required only for that portion distal to the hinge. The ventral surfaces of the cheliceral shafts cover the dorsal-lateral aspects of the prebuccal space (Figs. 2 and 5). The larger medial apophyses form a portion of the prebuccal roof (Fig. 5), and the heavy dorsolateral cuticular ridges on the cheliceral shafts close off the lateral, most posterior reflections of the prebuccal cavity by fitting snugly onto the dorsal rims of the palpal coxae (Figs. 2 and 4).

The labrum is a long tongue-like structure which lies between the ventromedial aspects of the chelicerae and extends anteriorly from the epistome approximately 27 microns (Figs. 2 and 5). The labrum is widest posteriorly and within its haemocoel is the labral retractor muscles and its long tubular tendon (Fig. 6). The labrum is also bulbous posteriorly and anteriorly tapers to a rather narrow tip (4 microns across). Anteriorly the labrum is roughly triangular in cross section (Fig. 6), and in its position between the chelicerae the broad ventral base serves to cover the medial-dorsal aspect of the prebuccal space (Figs. 2, 5, and 6). Posteriorly the ventral surface of the labrum fuses with the dorsal

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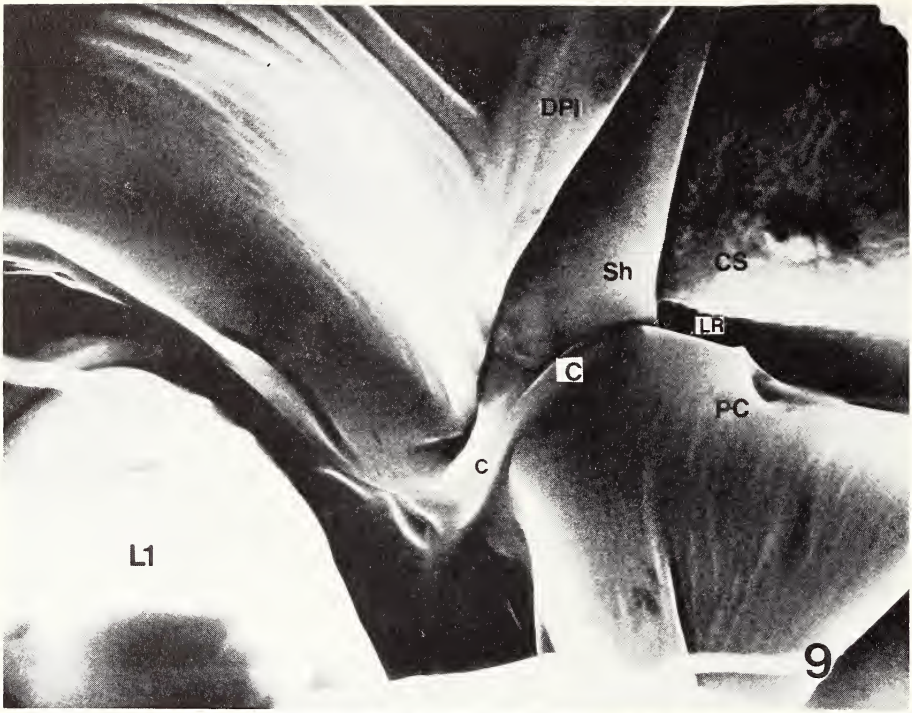
Fig. 7*a*. TEM of a cross section through the anterior pharyngeal region. At this level, lateral reflections (LR) of the alimentary canal have lost their communications with the external channel (C). The dilator muscles (DM) originate on the ventral surface of the epistome (E). × 2,000.

*b*. TEM of the lateral channel (C) at a more anterior level than in 7*a*. The lateral reflection (LR) is closer to the channel and still more anteriorly will form a continuous passage over the dorsal rim of the palpal coxa (PC). The external communication (*) of the channel is demonstrated. × 2,000.

Fig. 8*a*. SEM of an anteroventral view of the gnathosoma. The tips of the distal podomere (DP) are covered by hyaline cuticle; thus the three apical setae may not be observed by SEM. × 2,500.

*b*. Photomicrographs of the palpal podomeres. The tip of the distal podomere (DP) has three small setae, one is a solenidion (S) which is in a pit. × 800.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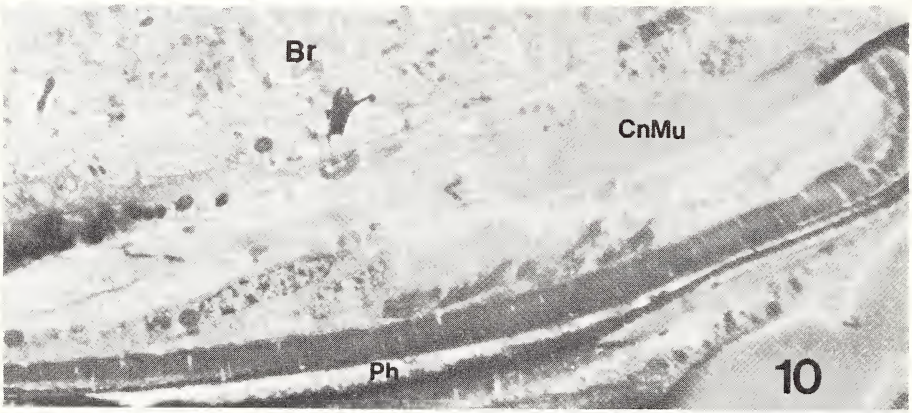
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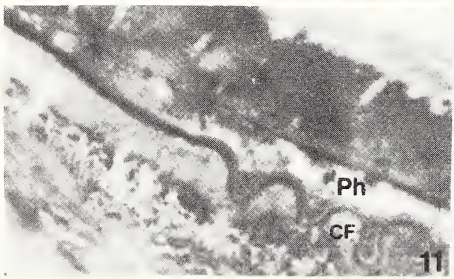
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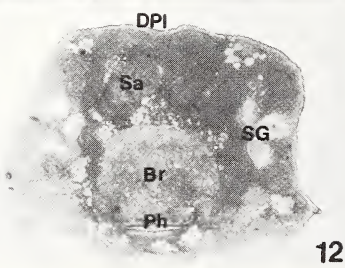
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wall of the pharynx while the dorsal surface of the labrum is continuous with the epistome. The epistome is a heavy apodeme which ventrally bears the origins of the pharyngeal dilator muscles (Fig. 5). It extends posteriorly approximately 30 microns and at its posterior limit, the labral retractor muscle has its origin. This internal sclerite forms the roof of the hypognathosoma.[5]

The hypostome forms the ventral face of the gnathosoma and lies between a pair of appendages, the pedipalps, whose large coxae form the posterior latero-ventral walls of the gnathosoma (Figs. 2 and 4). The hypostome consists of two portions, a median ridge and lateral elements which articulate with the ventromedial aspects of the palps (Fig. 2). A medial-ventral process of the hypostome that is independent of the palps extends anteriorly (22 microns) to a tip which is directed ventrally (Fig. 8*a*). On the dorsal surface of this tip are the most anterior extensions of two deep troughs (Fig. 8*a*) which run longitudinally between the median ridge of the hypostome and the palps (Fig. 2). The posterior limits of the troughs are just anterior to the level of the pharynx, and the troughs accommodate the movable digits of the chelicerae (Figs. 2 and 5). The lateral surface of the hypognathosoma is formed by the pedipalps (Figs. 2 and 4). The ventral hypognathosomal surface is heavily sclerotized and has one pair of anteriorly placed setae approximately 13 microns lateral to the midline. The dorsal surface of the median hypostomal ridge is regularly observed with two longitudinal folds and forms the floor of the prebuccal cavity (Figs. 5 and 6).

Each pedipalp consists of a large coxal segment which is fused insensibly both medially and ventrally to the hypostome, and two small podomeres (Fig. 4). The two podomeres of the palps are about 25 microns long and are oval in cross section. The basal podomere has two seta (one dorsal, one ventro-lateral) and is somewhat longer than the distal podomere (Figs. 4 and 8*a*). The distal podomere curves ventromedially and has one dorsal seta (Figs. 4

[5] A substitute word for subcapitulum of authors.

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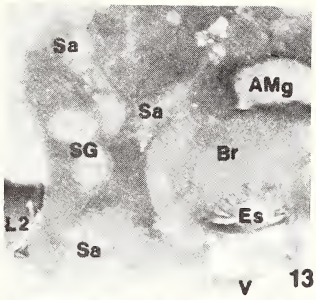
Fig. 9. SEM of a lateral view of the right side of the house-dust mite which demonstrates the course of the external channel (C) and where it communicates with the lateral reflection (LR) of the prebuccal cavity over the palpal coxa (PC). × 2,500.

Fig. 10. TEM of a cross section through the posterior pharynx (Ph) where the cuticle is rather thin and constrictor muscles (CnMu) are found. × 10,000.

Fig. 11. TEM of a cross section through the central phraynx (Ph) where the floor is ribbed by longitudinal cuticular folds (CF). × 10,000.

Fig. 12. Photomicrograph of a cross section through the region of the posterior pharynx (Ph) which underlies the brain (Br) at this level. A portoin of the dorsal salivary mass (Sa) is seen on the right side while several cells of the supracoxal gland (SG) are obvious on the left side of the mite. × 250.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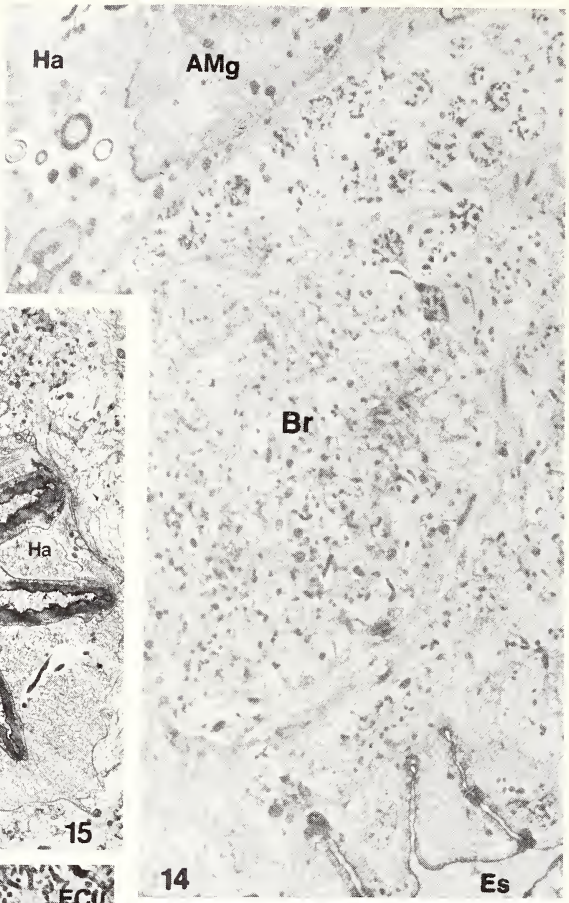
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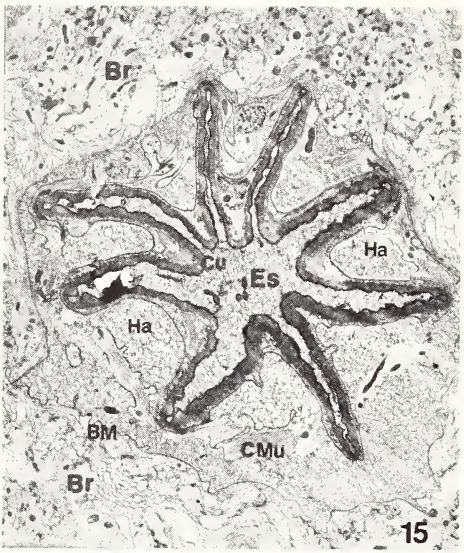
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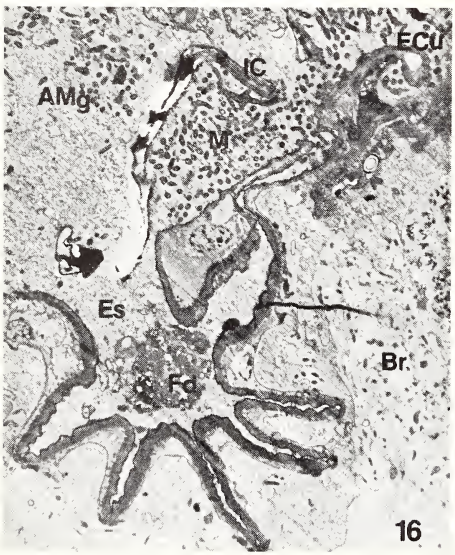
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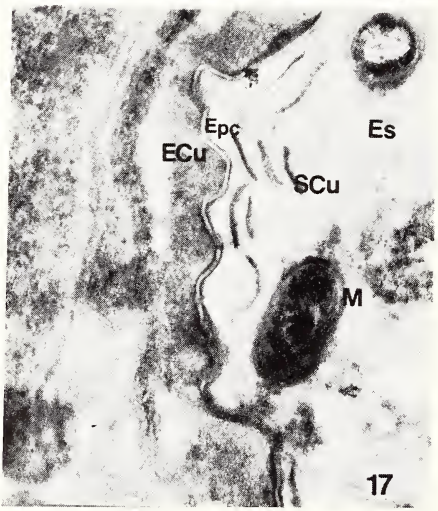
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and 8*a*). On the tip of the distal podomere are three rod-like setae which appear to be a single solenidian and two eupathidia (Fig. 8*b*); the solenidion (largest of the three) is ventral and is found in a pit, the smallest seta is dorsal, and all are covered by a hood of hyaline cuticle. The palps limit the most lateral aspects of the prebuccal cavity (Fig. 4). At the level where the hypognathosoma articulates with the idiosoma, a channel partially closed from the outside by a cuticular flap crosses over the dorsal margin of the palp (Fig. 9) and delivers glandular secretions into the prebuccal cavity.

The prebuccal cavity is not a permanently sealed compartment. It has a number of external connections. Not only is the cavity open between the labrum and hypostome but there are also dorsal openings between the chelicerae and lateral openings across the aforementioned troughs and over the dorsal rim of each palp (Fig. 2). The end of the prebuccal cavity and the beginning of the pharynx is at the level where the lateral reflections of the prebuccal space no longer have an external communication (Fig. 7*a*).

Two masses of glandular tissue located anterodorsally and one anteroventral mass can be seen within the idiosoma (Fig. 1). From the glandular masses, ducts run laterally and anteriorly to communicate with the channels that cross the palps and enter the prebuccal space (Fig. 7*b*). When the mite is standing in the usual position, the channel is located between the coxa of leg I and the gnathosoma and is difficult to observe (Fig. 9). Salivary secretions produced in the idiosoma are thus delivered to the prebuccal cavity. The salivary glands are intimately associated with the large supracoxal glands which open dorsal to coxa I (Fig. 13). In living mites mounted in mineral oil, the salivary glands appear to be made up of grapelike clusters.

The alimentary canal of *D. farinae* is separated into three main sections, each

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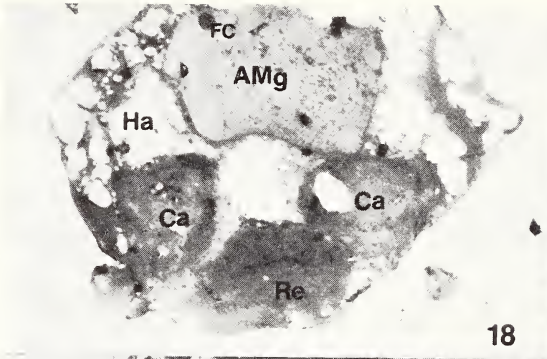
Fig. 13. Photomicrograph of a section at the level where the pharynx merges with the esophagus (Es) and the latter is becoming plicated. The anterior midgut (AMg) is now seen dorsal to the brain (Br) and elements of the salivary glands (Sa) are shown relative to cells of the supra coxal gland (SG). × 450.

Fig. 14. TEM of the anterior esophagus (Es) as it lies ventral to the brain (Br). Dorsal plications are obvious. × 4,000.

Fig. 15. TEM of a cross section through the central level of the esophagus (Es) as it passes through the midst of the brain (Br). Circular muscles (CMu) extend between the plicae. × 5,000.

Fig. 16. TEM of a section through the esophagus (Es) at the level where it protrudes into the anterior midgut (AMg) dorsal to the brain (Br). Flaps of esophageal cuticle (ECu) form a valve to prevent reverse peristalsis. Numerous unidentified microorganisms (M) are found in the gut of the house-dust mite. × 5,000.

Fig. 17. TEM of esophageal cuticle (ECu) which has a distinct epicuticle (Epc) and sloughed material (SCu) which may have originated from the cuticle. × 25,000.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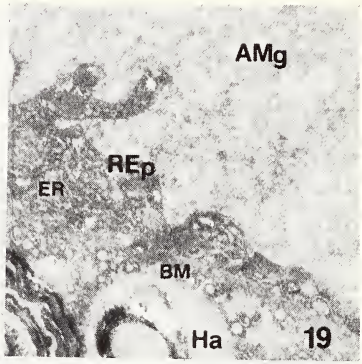
AMg
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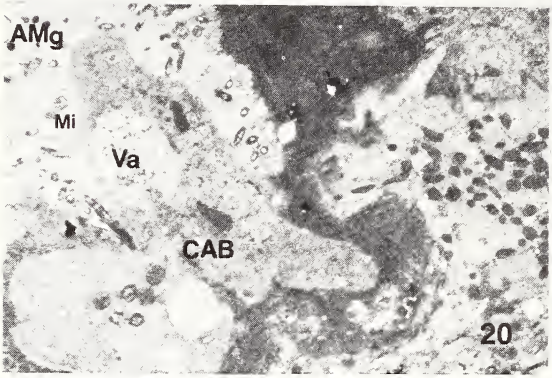
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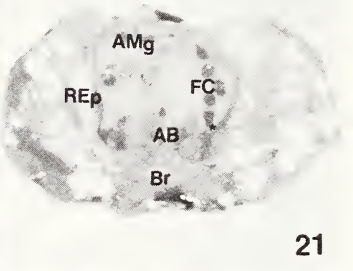
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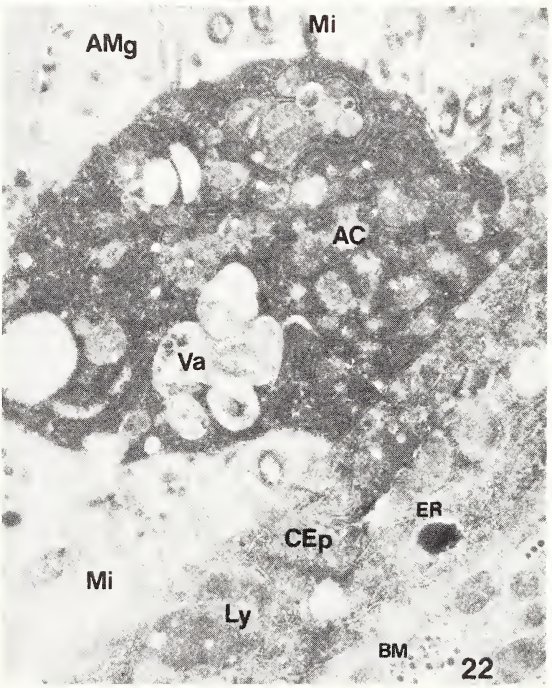
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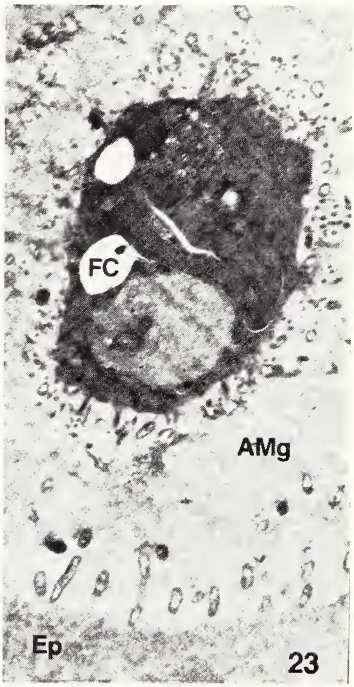
FC
AMg
Ep
23

of which can be subdivided at least once on morphological criteria. The three major regions are the foregut, midgut, and hindgut.

The foregut begins with the pharynx at the mouth or entrance to the alimentary canal. The pharynx, a muscular pump, is lined anteriorly with fibrous cuticle approximately 1 micron thick (Fig. 7*a*). The cuticle of the anterior portion of the pharynx has many pore canals. The pharynx is flattened and its lateral aspects curve dorsally (Fig. 12). Muscles are associated with the dorsal pharyngeal wall; five bands of dilator muscles originate on the ventral surface of the epistome and insert on the dorsal wall of the pharynx (Fig. 7*a*). Several bands of constrictor muscles originate medially on the dorsally curved lateral aspects of the pharynx and run transversely to the opposite medial side (Fig. 10). The most anterior constrictor muscle is found between the third and fourth dilator muscles, and the second constrictor is found between the fourth and fifth dilator. The remaining constrictor muscles are posterior to the dilators. The middle third of the pharyngeal floor is ribbed by longitudinal cuticular folds (Fig. 11), and posteriorly the cuticular pharyngeal lining becomes more heavily sclerotized and progressively thinner (to 0.75 micron). At the juncture of the pharynx and esophagus, the alimentary canal becomes highly plicated (Fig. 13).

The esophagus arises from the pharynx in the region of the brain. The dorsal wall of the pharynx comes in contact with the basement membrane of the brain as the ventral wall of the pharynx separates from the midventral wall of the idiosoma (Fig. 13). The dorsal wall of the alimentary canal becomes plicated as it is surrounded by nervous tissue (Fig. 14). These plications form grooves

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Fig. 18. Photomicrograph of a cross section through the anterior midgut (AMg) at a level where free portions of the caeca (Ca) can be observed. × 400.

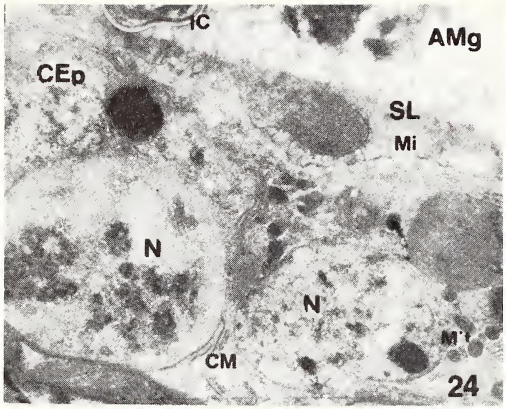
Fig. 19. TEM of the reduced epithelium (REp) which lines the dorsal-anterior region of the anterior midgut (AMg). These cells are reduced in apical-basal dimension. All gut epithelial cells are separated from the haemocoel (Ha) by a basement membrane (BM). × 12,000.

Fig. 20. TEM of a cell of the active bands (CAB) which line a portion of the ventral anterior midgut (AMg). Many cells of this type are found protruding into the gut lumen. × 2,500.

Fig. 21. Photomicrograph of a cross section which demonstrates the position of the active bands (AB) on the venter of the anterior midgut (AMg). Free cells (FC) in the gut lumen have originated from these bands, and one cell (*) was apparently fixed while in the process of becoming free. The remainder of the gut lining at this level is composed of reduced epithelium (REp). × 200.

Fig. 22. TEM of an attached cell (AC) about to become free in the gut lumen (AMg) but still adhering to the cuboidal epithelium (CEp) from which it originated. This cell appears to have undergone some degree of degeneration. × 8,000.

Fig. 23. TEM of a degenerating cell (FC) free in the lumen of the anterior midgut (AMg). × 4,000.


IC
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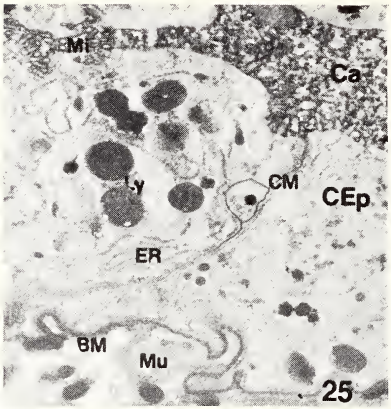
24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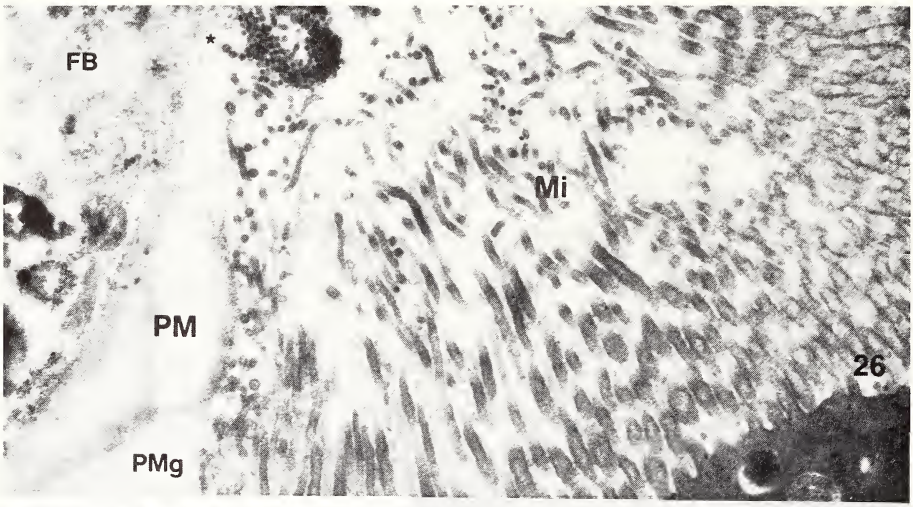
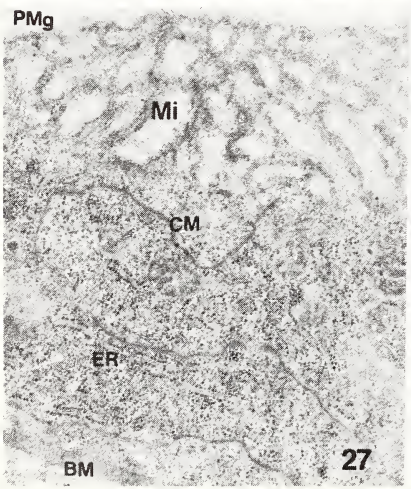

FB
*
Mi
PM
PMg
26


PMg
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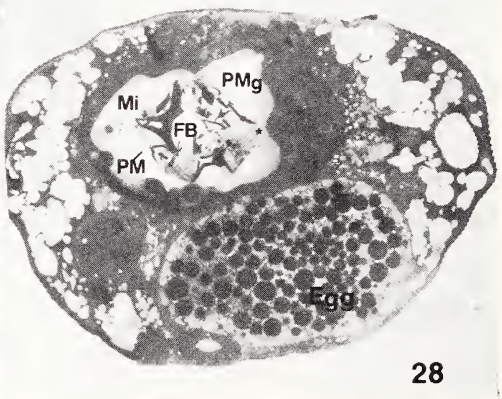
PMg
Mi
FB
PM
Egg
28

that become a part of the haemocoel (Fig. 15) so that a tubular extension of the haemocoel penetrates the brain from the level of the pharynx along the esophagus to the midgut. The nervous tissue is separated from this extension of the haemocoel by a well-defined basement membrane (Fig. 15). The plicated form of the alimentary canal as it is surrounded by the brain prevents the cerebral basement membrane from conforming to the outline of the gut epithelium (Fig. 15). As a result, the interface between brain and gut is filled with blood and connective tissue (Fig. 15). The entire esophagus passes in a dorsal direction through the midst of the brain (Fig. 15). The plications of the esophagus give it the appearance in cross section of an eight-pointed star. The central portion of the esophageal lumen is about 2.5 microns in diameter when collapsed. Each ray is about 0.25 micron wide at its tip and 0.8 micron wide at its base, and when expanded each ray would add approximately 10 microns to the total diameter of the esophagus. Thus the esophagus could accommodate particles over 20 microns in diameter. The lumen is lined by cuticle that is of almost uniform thickness (0.5 micron). Next to the lumen is a well-defined epicuticle that is 0.07 micron thick. Beneath the epicuticle, the rest of the cuticle seems to consist of exocuticle through which pore canals pass from the epithelial cells to the epicuticle. The pore canals are spaced 0.1 micron from each other and are about 0.42 micron in length. They appear to be unbranched and slightly larger in diameter at their interface with the epithelial cells. Constrictor muscles, limited from the connective tissue by basement membranes, are located between the plicae (Fig. 15) at one or more levels. In some specimens, portions of the epicuticular lining of the foregut have sloughed off in a laminar fashion (Fig. 17). The esophagus ultimately emerges dorsal to the brain and communicates with the midgut (Fig. 16).

The midgut of *D. farinae* is divided into an anterior and posterior region by a constriction (Fig. 1). The anterior region is approximately twice the size of the posterior section and is about 250 microns long. Extending posteriorly from

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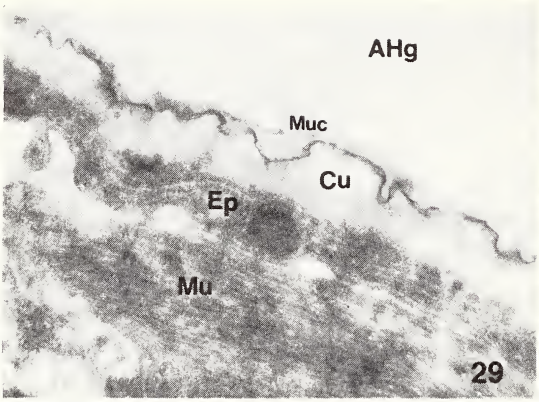
Fig. 24. TEM through the cuboidal epithelium (CEp) of the anterior midgut (AMg). The separating layer (SL) lies between gut contents and the epithelium. × 8,000.

Fig. 25. TEM of several cells which line the caecal lumen (Ca). Short microvilli (Mi) are numerous as are membrane-bound spheres interpreted to be lysosomes. × 6,000.

Fig. 26. TEM through the posterior midgut (PMg) at an anterior level where the long microvilli (Mi) are still partially adhering to the peritrophic membrane (PM). At the point of contact (*) the PM is relatively thin. × 12,000.

Fig. 27. TEM through the dense microvilli (Mi) of the posterior midgut (PMg). Rough endoplasmic reticulum (ER) is a characteristic of this epithelium. × 24,500.

Fig. 28. Photomicrograph of a cross section at the level of the posterior midgut (PMg). A peritrophic membrane (PM) surrounds a food ball (FB), and microvilli (Mi) which form the brush border contact the PM at its thinnest point (*) as in Fig. 26. × 450.


AHg
Muc
Cu
Ep
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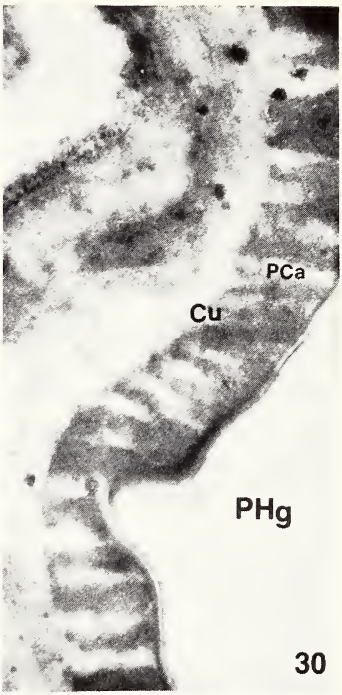
29


PCa
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PHg
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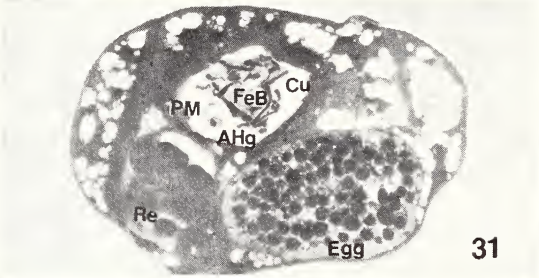
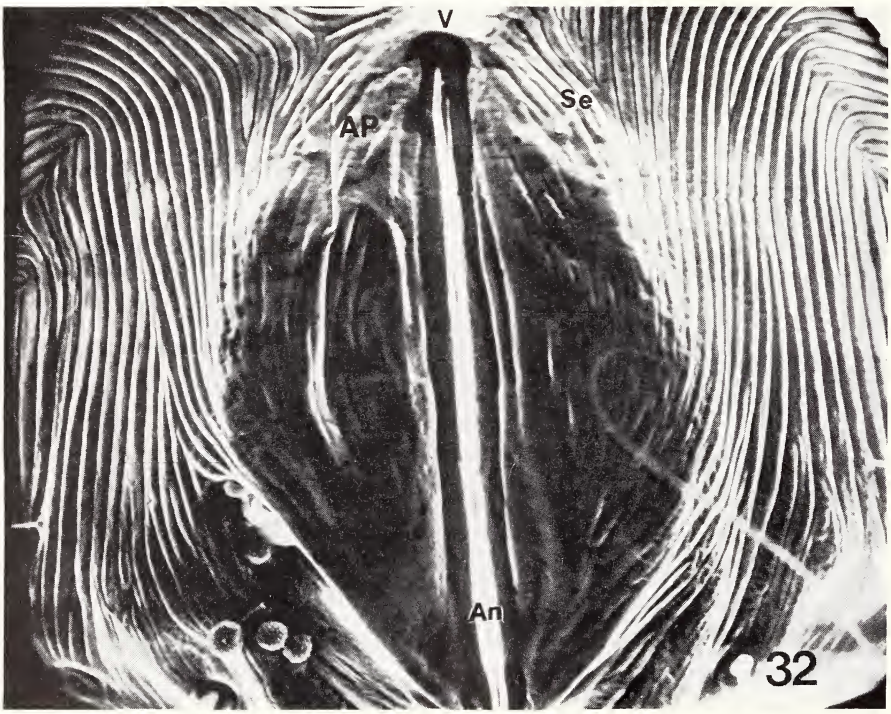

FeB
Cu
PM
AHg
Re
Egg
31


V
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AP
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32

the ventrolateral aspects of the anterior midgut are two diverticulae (caeca) which are about 150 microns long (Figs. 1 and 18). The midgut epithelium displays an interesting variety of cell types. The dorsal, most anterior, midgut epithelial cells are reduced in apical-basal dimension (Fig. 19). There are few microvilli, and common organelles such as mitochondria and nuclei are seldom observed. However, ventrally in this anterior region of the midgut are two rows of apparently active cells. Beginning at the point where the esophagus enters the midgut, the rows of active cells are evident all the way up to the constriction between the anterior and posterior midgut (Fig. 1). The cells of this region are characterized by a single nucleus, numerous short microvilli, rough endoplasmic reticulum, and large vacuoles (Fig. 20). It appears as though cells which are floating freely in the gut lumen have originated from ventral cell rows (Fig. 21). Some were apparently fixed while in the process of doing so (Figs. 21 and 22). The free cells in the gut lumen are generally round or elliptical in outline with many short microvilli, large vacuoles (both filled and empty), condensed endoplasmic reticulum, and remnants of other organelles which are difficult to positively identify (Fig. 23). Those cells which were fixed while in the process of becoming free from the midgut epithelium are typically narrow at their attached basal portion (Fig. 22) and rounded apically. The cytoplasm of these cells is in a state of degeneration which appears intermediate between that of the ventral row cells and that of the free cells in the gut lumen (Figs. 22 and 23).

More posteriorly, but still within the anterior region of the midgut, the dorsal and lateral epithelium is made up of cuboidal cells with short microvilli as well as a single nucleus, a few lysosomes, multivesicular bodies, mitochondria, and an extensive, rough endoplasmic reticulum (Fig. 24). Closely associated with the short microvilli of the cuboidal cells is a band of material which separates the contents of the gut from the epithelial cells (Fig. 24). Several of these cuboidal cells comprise active sites which appear to be located randomly along the epithelial lining of the anterior midgut. Many of the degenerating cells found free in the gut lumen are from these active sites (Fig. 23).

The cytoplasm of the cuboidal cells is also typical of the cells which line the

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Fig. 29. TEM through the cuticle (Cu) and thin underlying epithelium (Ep) of the anterior hindgut (AHg). A mucous-like lining (Muc) covers the cuticle. × 12,000.

Fig. 30. TEM through the cuticle (Cu) of the posterior hindgut (PHg). Numerous pore canals (PCa) are present. × 15,000.

Fig. 31. Photomicrograph of a cross section at the level of the cuticle-lined (Cu) anterior hindgut (AHg). A fecal ball (FeB) surrounded by a peritrophic membrane (PM) is seen in the gut lumen. × 300.

Fig. 32. SEM of a posteroventral view of the anal plates (AP) of the house-dust mite. Each plate has a single seta (Se). × 1,000.

caeca (Fig. 25). The cells of the caeca, however, have numerous electron-dense inclusions which are interpreted to be lysosomes (Fig. 25). The lumen of each caecum is quite constricted and appears occluded by flocculent materials as well as great numbers of microvilli. The caeca are limited from the haemocoel by a heavy basement membrane which appears to provide an attachment for circular muscles (Fig. 25).

The anterior and posterior sections of the midgut are separated by a constricted region (Fig. 1) which acts as a valve in allowing food to pass into the posterior section. In mites mounted in mineral oil, the valve is observed to expand and contract during the passage of food. At its narrowest point, the diameter of the valve has been measured at 20 microns compared with a diameter of 100 microns for the anterior midgut and 85 microns for the posterior midgut. The lumen of the valve is practically obscured by long microvilli (Fig. 1), and all food material must pass through this region in the process of being included in a food ball.

The posterior region of the midgut has long microvilli (up to 3.5 microns). An obvious peritrophic membrane surrounding individual food balls is noted in this region (Figs. 26 and 28). Where the food is adpressed to the long microvilli of the posterior midgut, the peritrophic membrane is at its thinnest (Fig. 26). By the time the food has moved posterior to the valve and is free of the microvilli, the thicker peritrophic membrane has completely encased the food to form a food ball (Fig. 28). As well as long microvilli, the posterior midgut cells have an extensive, rough endoplasmic reticulum (Fig. 27), and other organelles typical of an actively secreting cytoplasm are observed.

The posterior midgut and the anterior hindgut are separated by a slight narrowing of the alimentary canal between the two regions (Fig. 1). No muscles have been found associated with this constriction, and the regular contractions noted in the more anterior valve were not observed here. Contractions which move food balls from the midgut to the hindgut are initiated in the posterior midgut and proceed less vigorously since no valve is involved.

The anterior and posterior regions of the hindgut are lined with cuticle (Fig. 1). Longitudinal folds in this cuticle run the entire length of the anterior hindgut and in cross section appear as indentations in the cuticle (Fig. 29). The cuticle of the anterior region (1.0 micron thick) may be covered by a substance which has the appearance of a mucous-like lining (Fig. 29). Although it is impossible to determine the exact composition of this material after utilizing basic TEM techniques, it has been noted that the material is electron-dense, homogeneous, and if present fills the many indentations of the hindgut cuticle (Fig. 29). Endoplasmic reticulum is often found in the hypodermis which underlies the hindgut cuticle (Fig. 29). What appear to be contractile cells have also been

seen (Fig. 29). Peritrophic-membrane-wrapped fecal material is observed in the hindgut (Fig. 31). This fecal material often contains the cuticle of ingested portions of mites. No valve was observed between the anterior and posterior hindgut; these cuticle-lined sections merely merge where the lumen narrows and the pore canals of the posterior hindgut become obvious.

The cuticle of the posterior hindgut generally has many pore canals (Fig. 30). The cuticle surrounds a narrow lumen only about 2.5 microns in diameter. The posterior region of the hindgut terminates at a pair of anal plates which together form an oval about the slit-like anus on the posteroventral aspect of the mite. Each plate has a single, anteriorly placed seta (Fig. 32).

## DISCUSSION

Common to all orders of Acari is a gut divided into six more or less well-defined regions. Reuter (1909) has described four types of Acarine digestive systems, while Vitzthum (1940) considers three types, calling the gut of the Tetrapodili a special case (see Whitmoyer *et al.*, 1972, for a recent example). Mitchell and Nadchatram (1968) have also described a specialized gut in the chigger mites. However, all authors seem to agree on the use of the term pharynx for the muscular, cuticle-lined pump which anteriorly begins the alimentary canal, and the term esophagus for the cuticle-lined tube which leads posteriorly from the pharynx through the brain to the midgut. The remaining four gut regions of the Acari show great variation in form and nomenclature (Table 1).

The esophagus is followed by a sac-like, epithelial-lined structure commonly labeled a stomach or ventriculus which may have two or more diverticulae (caeca). The next section of the gut is a second epithelial-lined region which has considerable morphological variety and a matching lack of uniformity in nomenclature, e.g., colon, intestine, hindgut, posterior midgut. If present, excretory tubules are located posterior to this latter region and anterior to the next region. The two posterior sections of the gut may be lined wholly or in part by cuticle and have been named hindgut, rectum, post-colon, and anus in varying combinations.

A great deal of variety also exists in the literature concerning the naming of the gut regions of acarid mites. There are three main sections of the gut to be considered, the foregut, midgut, and hindgut. In most cases, however, investigators of acarid mites have avoided the use of fore-, mid-, and hindgut. The digestive systems of several free-living relatives of *D. farinae* have been described, and the gut regions demonstrated are strikingly similar in each case. The foregut is regularly described as consisting of an anterior pharynx followed by the esophagus. The remaining gut is then divided into three or four sections (Table 1).

Table 1. The nomenclature as proposed by authors for divisions of the digestive systems of several mites (with special reference to the Acaridei). The homologies of the gut regions may be identified in the corresponding vertical columns. The first three authors do not use the fore-, mid-, and hindgut designations; the final three authors do so categorize the gut regions.

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| Vitzthum (1940) Acaridei | pharynx | esophagus | midgut | intestine | colon | rectum | anus |
| Michael (1901) *Glycyphagus platygaster* | pharynx | esophagus | ventriculus | colon | | rectum | anus |
| Kuo & Nesbitt (1970) *Caloglyphus mycophagus* | pharynx | esophagus | stomach | colon | rectum | | anus |
| | *foregut* | | *midgut* | | *hindgut* | | |
| Brody, McGrath, and Wharton *Dermatophagoides farinae* | pharynx | esophagus | anterior midgut | posterior midgut | anterior hindgut | posterior hindgut | anus |
| Prasse (1967) *Caloglyphus berlesei* | pharynx | esophagus | ventriculus | colon | post-colon | rectum | anus |
| Evans, Sheals, and Macfarlane (1961) all mites | pharynx | esophagus | stomach or ventriculus | intestine | | rectum | anus |

Homologies of the gut regions have been considered by a number of investigators. All authors agree on the terms pharynx and esophagus (Table 1). Michael (1901) studied a number of acarid mites and has had a significant influence on the anatomical nomenclature. For *Glycyphagus platygaster* (syn. *Labidophorus talpae* Kramer, 1877), he divided the gut into three sections, a ventriculus, colon, and rectum (Table 1). Several investigators have followed this pattern, and subsequent difficulties in naming the gut regions have arisen because of the anatomical variation in the acarid mites. Furthermore, the use of fore-, mid-, and hindgut categories are used by some authors and ignored by others (Table 1). Two morphological criteria may be recognized for naming the gut regions posterior to the foregut, the presence or absence of a cuticular lining and the location of Malpighian tubules. If present, the Malpighian tubules enter the gut at the juncture of the mid- and hindguts. Prasse (1967) found that the chamber posterior to the colon of *Caloglyphus* had a lining of cells characterized by a striated border. Because of this he referred to this posterior region as the post-colon and included it as a portion of the midgut (Table 1). Using the criterion based on presence or absence of cuticle this is an appropriate decision, but it places the Malpighian tubules between two sections of the midgut. Malpighian tubules are reported in a number of acarid mites, but Michael (1901) and Vitzthum (1940) have indicated several species with no apparent excretory tubules. *D. farinae* fits into the latter category; no Malpighian tubules have been observed.

The division of the gut into the three primary regions (of foregut, midgut, and hindgut), using the criterion of presence or absence of cuticle, is followed in this study of *D. farinae*. The gut of *D. farinae* has a cuticular lining on both posterior regions and so both are designated as hindgut. The anterior region of the hindgut is homologous to the post-colon of *Caloglyphus* (Prasse, 1967) but differs from it by having a cuticular rather than an epithelial lining. Certainly the terminology for homologous regions should be uniform. In many acarid mites, the presence of Malpighian tubules can be used to delimit the division between mid- and hindgut. The fact that the use of this criterion for the acarid mites leads to the same divisions as the cuticular criterion does in pyroglyphid mites suggests that it should be used, and that the post-colon should be recognized as the anterior region of the hindgut.

A developmental definition of fore-, mid-, and hindgut, equating them as derivatives of stomodaeum, endoderm, and proctodaeum, respectively, has been used in the past without extensive confirmatory developmental studies. The embryology of gut formation in insects has been discussed by Sharov (1966). He reports the formation of microvillate epithelium from the stomodaeum and proctodaeum, thus claiming the ectodermal origin of the entire alimentary canal at least in some cases. Certainly his findings suggest that a developmental definition of the fore-, mid-, and hindgut regions is at best questionable.

It seems that many authors (e.g., Evans, Sheals, and Macfarlane) followed Michael's implication that everything behind the ventriculus was hindgut. Certainly Michael's use of the term colon could be interpreted in this manner. This confusion has persisted, but it is hoped that it will be dispelled in time. In the acari, the midgut is usually divided into two regions. Up to now at any rate, the entrance of the Malpighian tubules into the gut seems to be a certain landmark for differentiating between mid- and hindgut in those forms that have tubules. Using this criterion, no acarine is known to have more than one transverse division of its midgut.

In *D. farinae*, ingestion begins with mouthparts specifically designed for manipulating solid particles. The large dentate chelicerae, with the medial apophyses fitting snugly over the prebuccal space (Fig. 5), tear off and pick up pieces of food that are placed in the buccal region. The chelicerae move in an anterior-posterior direction in such a manner that when one chelicera is extended forward the other is pulled back. The food material which has been placed in the buccal space by the chelicera that is moving forward is now pushed posteriorly by the retracting food-laden chelicerae of the opposite side. In this manner the prebuccal space of a feeding mite is filled with food. The prebuccal cavity must then be sealed from the outside so that the pharyngeal pump can suck the food material back, presumably in a bath of digestive juice secreted by the salivary glands. The prebuccal region may be sealed anteriorly by the labrum, dorsally by the labrum and chelicerae, and laterally by the cuticular ridges on the chelicerae which can be adpressed to the dorsal margins of the palps. The prebuccal cavity and pharynx are capable of great distension, allowing appendages (of other mites) with a diameter up to 20 microns to be ingested. The cuticle-lined, distensible foregut (Fig. 15) can accommodate large pieces of food passing into the midgut for digestion. The pharyngeal dilators and constrictors are antagonistic muscles (Johnston, 1965), and their alternate contractions result in the pumping action of the pharynx. On the other hand, only circular muscles, which are interpreted to be constrictors, have been found associated with the esophagus (Fig. 15). This suggests a peristaltic action for the latter. The pharyngeal pump, closed as described above, forces material back into the esophagus which is plicated when empty. The constrictor muscles, upon distension of the esophagus, may then act in sequence to move the food along the tract and into the midgut.

Studies concerning the digestive functions of several arachnids have indicated that the midgut epithelium carries out post-oral food processing and absorption by intracellular digestion (Bader, 1938; Phillipson, 1961; Wright and Newell, 1964; Mitchell, 1970). This study offers evidence of extracellular as well as intracellular digestive processes within *D. farinae*. The intracellular process requires an engulfing of food material by the individual midgut cells. Intracellular digestion takes place in cells that are at some time sloughed off into the

gut lumen and are eventually decomposed. The midgut may actually be filled with free-floating gut cells (Phillipson, 1961; Wright and Newell, 1964).

The house-dust mite ingests fluids, but it also takes in relatively large, solid particles. In its most common habitat, the human abode, *D. farinae* is reported to live on sloughed epidermal cells (Larson *et al.*, 1969). In culture, yeast is provided as food, but in the absence of other food, cannibalism is common among house-dust mites. Consequently, one may assume that *D. farinae* has evolved a method of ingesting large pieces of keratinized (dander) or sclerotized (cuticle) material. In the anterior midgut and possibly the caeca, these ingested particles are suspended in a flocculent mass of food (Fig. 24) which apparently undergoes intracellular digestion. This assumption is based on the presence of numerous degenerating cells which have been sloughed off into the gut lumen (Figs. 21 and 23) or are in the process of pinching off and degenerating before being lost from the epithelial lining (Fig. 22). These cells, both attached and free, have clear cytoplasmic regions which may be food vacuoles (Fig. 20). An extensive supply of rough endoplasmic reticulum, plus food vacuoles, may indicate an intracellular digestive process in the anterior midgut. On the other hand, food vacuoles have not been observed in the caecal cells, nor has particulate material been seen in the caecal lumen. This may suggest an extracellular digestive process. Furthermore, the presence of circular muscles (Fig. 25) surrounding the caeca may indicate that enzymes produced there are squeezed anteriorly to be made available for extracellular digestive processes in the midgut.

However, the digestive process may not be completed in the anterior midgut. It appears impractical for a midgut cell to engulf pieces of material as large and ragged as those seen in the gut lumen. Therefore it is suggested that some degree of extracellular digestion may occur in the posterior midgut of *D. farinae*. Prasse (1967) and Akimov (1971) have reported digestive processes in the post-colon of *Caloglyphus* and *Rhizoglyphus* respectively.

Prior to further consideration of extracellular digestion, it is necessary to point out that the function of the dorsal anterior midgut cells, other than their role of maintaining continuity of the digestive tract, is not clear. This area in insects is described as a site of peritrophic membrane production (Peters, 1969; Richards and Richards, 1971), but there is nothing in this study of *D. farinae* to indicate a similar function for this region. The ventral bands as well as all the posterior cells of the anterior midgut have cytoplasm which appears to be active (Figs. 20 and 24).

Considering the pieces of cuticle which are commonly found in the midgut, some form of protection for the midgut epithelium is appropriate. Consequently, there is the peritrophic membrane (PM) which envelops the food material as it is pushed through the valve between the anterior and posterior midgut (Wharton and Brody, 1972). It is difficult to determine the precise origin of the PM, but its components may be produced in different regions of the gut as

has been proposed for some insects (Smith, 1968). In *D. farinae*, situated between the microvilli and the contents of the anterior midgut lumen, is a band of electron-dense material (up to 4.5 microns thick) that may contribute to the formation of the peritrophic membrane in the posterior midgut (Fig. 24). There is also the peculiar laminated material which has sloughed off in the foregut (Fig. 17), which may be another component of the PM. It does seem clear, however, that the PM takes its final form at the juncture of the anterior and posterior midgut and is there consolidated into a sheet completely surrounding a food ball (Fig. 28). The PM remains evident around the feces in the hindgut as well (Wharton and Brody, 1972) and is ultimately excreted in a fecal pellet composed of 3 to 5 processed food balls.

The presence of a peritrophic membrane in the posterior midgut of *D. farinae* precludes any further intracellular digestion of particulate material from taking place. Furthermore, the posterior midgut epithelium has cells with extremely long, often densely packed microvilli (Figs. 26 and 27), and this may be the region of most active nutrient absorption as the greatest cell surface is offered here. These cells are typically replete with rough endoplasmic reticulum (Fig. 27). The presence of endoplasmic reticulum, in addition to multivesicular bodies, lysosomes, and other organelles typical of a secretory cell, suggests that extracellular digestion may be occurring in the posterior midgut of *D. farinae*. A few free cells, similar to those in the anterior midgut, have been observed in the posterior midgut, but outside of the peritrophic membrane (Fig. 28). Assuming that no food is available outside the PM, the function of these free cells is questionable.

The peritrophic membrane-wrapped fecal material then passes posteriorly down the hindgut where some degree of water resorption probably takes place. While it has been noted that the cuticle of the posterior hindgut has numerous pore canals, it is yet to be determined what form of water-regulatory mechanism the house-dust mite utilizes. The type of epithelium found here is unlike that of the water-resorptive epithelium in many insects (Oschman and Wall, 1969). The fecal pellet of *D. farinae* (containing 3 to 5 individual balls) is held together presumably by the mucous-like material which is often observed covering the hindgut cuticle (Fig. 29). The fecal pellets remain intact in air, but break up in mineral oil.

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